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Advancing research on alien species and biological invasions

Alien ants (Hymenoptera, Formicidae) on a quest to conquer Greece: a review including an updated species checklist and guidance for future research

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Abstract

Biological invasions represent one of the main drivers of biodiversity loss with adverse impacts on human societies, economies and public health. More than 500 ant species have been transported outside their native range with the help of humans, while the majority of them have managed to establish viable populations in the wild. Nevertheless, data from the Mediterranean region suggest that most alien ants occupy anthropogenic habitats with little spread in semi-natural and natural habitats. Research on biological invasions of ants in Greece had previously identified a total of 15 alien ant species. In this article, an extensive literature investigation and material examination provide a revised checklist of the alien myrmecofauna of Greece. Although the number of alien ant species remains the same, the checklist's composition is largely altered to provide an up-to-date overview of the country's alien myrmecofauna in order to enhance management decisions and future research. The presence and distribution of alien ants within Greek administrative divisions, NATURA 2000 sites and Corine Land Cover types are analysed and presented. In particular, the species richness of alien ants seems to be highest in the Aegean Archipelago (Crete and Southern Aegean Islands) probably due to uneven collecting efforts and increased climatic suitability. Alien ant species are mostly associated with anthropogenic habitats including urban and agricultural areas, although

a significant percentage has managed to spread into forest and semi-natural areas, including protected NATURA 2000 sites. Future research directions enhancing the monitoring of alien ants and their impacts are indicated to safeguard native ant biodiversity and conservation efforts of rare and endemic taxa.

Keywords
alien species, biological invasions, *Cardiocondyla obscurior*, first record, invasive alien species, social insects, tramp species

Introduction

The main drivers of global change such as invasive alien species, climate change, land-use change and pollution have been found to synergistically exacerbate global biodiversity loss, both directly and indirectly (Butchart et al. 2010; IPBES 2019). Scientists around the world have warned about the adverse impacts of invasive alien species towards native biodiversity and ecosystem functioning, biogeographic patterns and species' extinction rates, as well as impacts on public health and socio-economic parameters, calling for international cooperation and stronger biosecurity regulations to mitigate their impacts (Bacher et al. 2018; Mazza and Tricarico 2018; Pyšek et al. 2020). Approximately 14,000 alien species have been identified in Europe, with a large proportion of them being insects (EASIN 2022). Alien terrestrial invertebrates are mostly synanthropic, predominantly invading man-made habitats such as parks and gardens, buildings, agricultural land and greenhouses (Lopez-Vaamonde et al. 2010). Although protected areas have been characterised as more resilient to biological invasions, established populations of alien species can be found lurking in their boundaries (Gallardo et al. 2017; Liu et al. 2020).

More than 500 species of ants have been transferred outside their native range and successfully bypassed biosecurity controls, with almost two thirds of them managing to establish populations in the wild (Wong et al. 2023). The global costs of invasive ants have been recently estimated at around 51.93 billion USD annually, however, these numbers are perceived as severely underestimated and there is a call for improved cost reporting (Angulo et al. 2022). Although 17 ant species have been identified as harmful towards native biodiversity and ecosystem function (Wong et al. 2023), more than 80% of worldwide invasion costs correspond to only two species [i.e. *Solenopsis invicta* Buren, 1972 and *Wasmannia auropunctata* (Roger, 1863)] (Angulo et al. 2022). Recent studies addressing alien ants in the Mediterranean have identified around 40 species, mostly invading anthropogenic habitats although the extent of natural and introduced range of some species [e.g. *Cardiocondyla mauritanica* Forel, 1890, *Monomorium subopacum* (Smith, F., 1858)] is somewhat problematic (Schifani 2019). The European Alien Species Information Network (EASIN) currently lists 65 species of ants as alien to or within Europe (EASIN 2022).

The first lists of alien ants in Greece were published by Salata et al. (2019) and Schifani (2019), including 15 and 14 species, respectively. Out of the 14 species

mentioned in Schifani (2019), Salata et al. (2019) had excluded *Aphaenogaster splendida* (Roger, 1859) and *Monomorium monomorium* Bolton, 1987 [previously reported as alien to Greece by Salata and Borowiec (2018), although questionable according to Schifani (2019)], while also adding records of *Nylanderia vividula* (Nylander, 1846), *M. subopacum* and *S. geminata*. Furthermore, Salata et al. (2019) questioned records of *Anoplolepis gracilipes* (Smith, 1857) (Radchenko 2007) and *Pheidole megacephala* (Fabricius, 1793) (Borowiec and Salata 2012). Later, Demetriou et al. (2021) revised the checklist of alien insects inhabiting Greece, listing a total of 15 ant species, strongly resembling that of Salata et al. (2019), although excluding *Hypoponera eduardi* (Forel, 1894) and adding *Lasius neglectus* van Loon, Boomsma & Andrásfalvy, 1990 (Salata and Borowiec 2019b).

In this publication, the checklist of alien ants of Greece is revised including notes on their distribution and providing reasons on why some species were excluded. Literature and distribution maps are presented for each species. Additionally, georeferenced records are analysed in the context of their presence within the NATURA 2000 network and land cover. Lastly, future research directions are discussed.

Materials and methods

Data collection and specimen identification

Records of alien ant species reported from Greece were searched through AntMaps (Janicki et al. 2016; Guénard et al. 2017), available scientific literature (Forel 1886, 1910; Collingwood 1993; Seifert 2003, 2020; Bolton and Fischer 2011; Borowiec and Salata 2012, 2013, 2014, 2017, 2018a, b, d, 2021a; Seifert et al. 2017a, b; Wagner et al. 2017; Salata and Borowiec 2018, 2019a, b; Salata et al. 2019, 2020; Tseng et al. 2019; Borowiec et al. 2021, 2022) and were subsequently catalogued. In addition, samples in the collections of L. Borowiec and S. Salata (Department of Biodiversity and Evolutionary Taxonomy, University of Wrocław, Poland – **DBET**), and Ch. Georgiadis (Museum of Zoology of the University of Athens, Greece – **ZMUA**) including both published and unpublished material were included. Identifications were based on the largest collection of Balkan ants preserved in the Museum of Natural History, University of Wroclaw, Poland – **MNHW**, knowledge resulting from studies on this collection in the last 12 years, comparative studies on types of European ants and several earlier regional works on European ants such as Agosti and Collingwood (1987), Czechowski et al. (2012), Seifert (2018), and recent revisions for genera and species complexes/groups e.g. Wagner et al. (2017) for the *Tetramorium caespitum* group, Seifert (2003) for the genus *Cardiocondyla*, Seifert et al. (2017a) for the *Tapinoma nigerrimum* group, and Seifert (2020) for the genus *Lasius*.

The native range of species was assessed based on available scientific literature, although in some cases their native range has been characterized as "questionable" or even "unknown" e.g. that of *A. splendida* (Schifani 2019) or *L. neglectus* (Stukalyuk et

al. 2020). Assessment criteria in Essl et al. (2018) were used to evaluate whether a species could be regarded as native or alien to Greece. In cases where a species was previously characterized as alien (i.e. *H. eduardi*, *M. monomorium* and *M. subopacum*) but failed to demonstratively have crossed a biogeographic barrier to enter the country via human activities, this was regarded as native to the country. In addition, the habitats occupied by the assessed species were also taken into consideration with species such as *H. eduardi* that can be found in natural habitats under specific habitat requirements being considered as native.

According to their establishment status, alien ants were catalogued as Established i.e. "non-native species records with established populations in the wild" or Indoors introduced i.e. "non-native species records without established populations in the wild (e.g. in buildings, greenhouses, airport, quarantine surveys)", as per AntMaps categories: exotic and indoors introduced (Janicki et al. 2016; Guénard et al. 2017). Lastly, the establishment status of data-deficient species is regarded as "Unknown". Species excluded from the checklist are discussed.

Data analysis and visualisation

The distribution of alien ant species within the 14 Greek administrative divisions (Kallikratis Programme) was analysed and mapped, calculating their area of occupancy (AOO) in a 2 × 2 km^2 grid, the number of occupied administrative divisions as well as the year of first published official record for each alien ant species reported from Greece. A total of 191 georeferenced observations (Suppl. material 1) were pooled in QGIS Version 3.18.2 free and open source Geographic Information System (https://qgis.org/en/site/) and were assigned to their respective land cover and presence within the NATURA2000 network. Boundaries and habitat types were based on the European layers of Corine Land Cover (CLC) project version CLC2018 and NATURA2000 sites, downloaded from Copernicus Land Monitoring Service and the European Environmental Agency, respectively. According to the Copernicus Land Monitoring Service, records within the following land-cover types were mapped: artificial surfaces, agricultural areas, forest and semi-natural areas, wetlands and water bodies as well as their respective sub-categories (https://land.copernicus.eu/user-corner/technical-library/corine-land-cover-nomenclature-guidelines/html). Since CLC2018 files had an accuracy of 100 m, georeferenced records with only two decimal digits or less in latitude and/or longitude fields, were excluded from CLC and NATURA 2000 analyses to retain a higher accuracy. Thus, a total of 169 georeferenced records were assigned to their corresponding CLC types and mapped for presence within the NATURA 2000 network.

Specimen photography

Photographs of specimens, unless stated otherwise, were taken by Prof. Lech Borowiec using Nikon SMZ18 and Nikon SMZ 1500 stereomicroscopes, Nikon D5200 camera and Helicon Focus software.

Results

Biodiversity and distribution

The revised checklist of the alien myrmecofauna of Greece currently includes fifteen (15) species distributed in four (4) subfamilies (Table 1). A total of eight (8) species regarded as alien in Greece were excluded from previous publications as they represent misidentifications or proved to be native to the country. In greater detail, following Salata et al. (2019) and Schifani (2019), *Anoplolepis gracilipes*, *Aphaenogaster splendida*, *Monomorium monomorium*, *Nylanderia vividula*, *Pheidole megacephala*, and *Solenopsis geminata* are removed from previous checklists as dubious records while *Hypononera eduardi* and *Monomorium subopacum* were proved to be native. *Cardiocondyla obscurior* Wheeler, 1929, is presented for the first time for Greece.

The majority of the species have been detected in Southern Greece and its islands, with the South Aegean Islands and Crete hosting a total of 11 and 10 alien ant species, respectively (Fig. 1). North Aegean Islands follow with six species while the Ionian Islands and the Peloponnese each hold five species. In the remaining regions, fewer than four species have been identified whereas Mount Athos and Western Macedonia hold no records of alien ants (Fig. 1).

Tetramorium immigrans seems to be widely distributed, inhabiting ten out of 14 administrative divisions of Greece (Table 2). *Nylanderia jaegerskioeldi*, *Pheidole indica* and *Cardiocondyla mauritanica* follow occupying seven, six and five administrative divisions in Southern Greece and Greek islands, respectively. Alien species found in just one administrative division include *C. obscurior* and

Table 1. Updated checklist of the alien myrmecofauna of Greece, including their origin and establishment status.

No.	Subfamily	Tribe	Species	Origin	Establishment status
1	Dolichoderinae	Leptomyrmecini	*Linepithema humile* (Mayr, 1868)	Neotropics	Established
2		Tapinomini	*Tapinoma magnum* Mayr, 1861	W. Mediterranean	Established
3	Formicinae	Lasiini	*Lasius neglectus* Van Loon, Boomsma & Andrasfalvy, 1990	C. Asia	Established
4			*Paratrechina longicornis* (Latreille, 1802)	Indomalaya	Established
5			*Nylanderia jaegerskioeldi* (Mayr, 1904)	Africa	Established
6		Plagiolepidini	*Lepisiota syriaca* (André, 1881)	Near East	Established
7	Myrmicinae	Attini	*Pheidole indica* Mayr, 1879	Indomalaya	Established
8			*Strumigenys membranifera* (Emery, 1869)	Sub-Saharan Africa	Unknown
9		Crematogastrini	*Cardiocondyla mauritanica* Forel, 1890	Palearctic – N. Africa	Established
10			*Cardiocondyla obscurior* Wheeler, 1929	Indomalaya	Unknown
11			*Tetramorium bicarinatum* (Nylander, 1846)	Indomalaya	Established
12			*Tetramorium immigrans* Santschi, 1927	Anatolia and Caucasus	Established
13		Solenopsidini	*Monomorium bicolor* Emery, 1887	Africa	Established
14			*Monomorium pharaonis* (Linnaeus, 1758)	Africa	Indoors introduced
15	Ponerinae	Ponerini	*Hypoponera punctatissima* (Roger, 1859)	Sub-Saharan Africa	Established

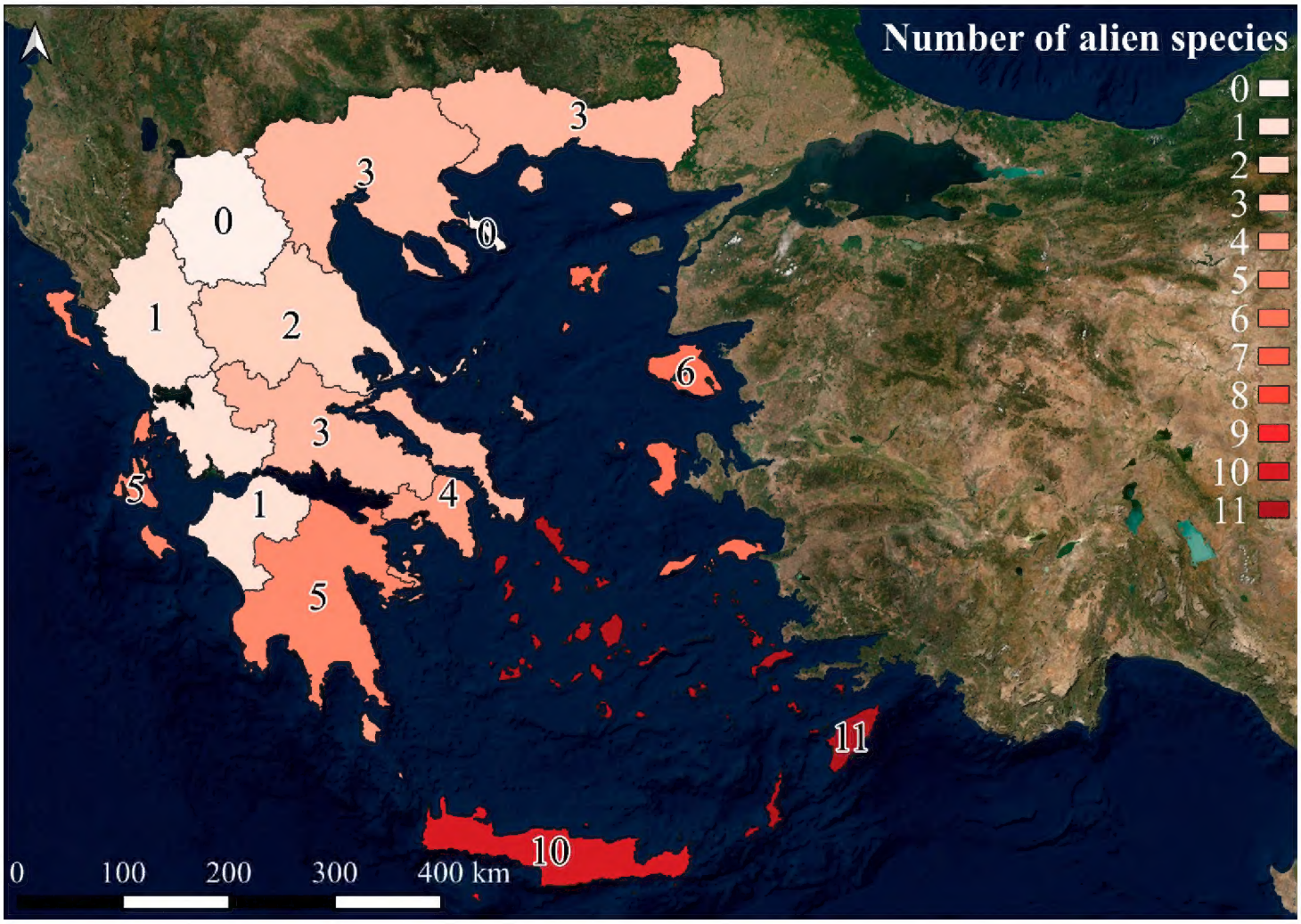

Figure 1. Number of alien ant species in each Greek administrative division.

Table 2. Area of occupancy (AOO), number of occupied administrative divisions and year of first published official record for each alien ant species reported from Greece.

Species	AOO (km²)	Number of adm. divisions occupied	Year of first official record (published)
Cardiocondyla mauritanica	60	5	2003
Cardiocondyla obscurior	4	1	2023
Hypoponera punctatissima	4	2	1987
Lasius neglectus	92	4	2016
Lespisiota syriaca	16	3	1928
Linepithema humile	16	4	1967
Monomorium bicolor	68	2	1928
Monomorium pharaonis	N/A	3	1928
Nylanderia jaegerskioeldi	128	7	1932
Paratrechina longicornis	20	1	1988
Pheidole indica	104	6	1910
Strumigenys membranifera	N/A	1	1987
Tapinoma magnum	20	3	2022
Tetramorium bicarinatum	8	1	2019
Tetramorium immigrans	144	10	2017

Paratrechina longicornis in South Aegean, *S. membranifera* collected from Epirus (Salata and Borowiec 2018) and *Tetramorium bicarinatum* known only from the island of Crete (Salata et al. 2020).

Land-use and presence in protected areas

The presence of nine alien ant species within the NATURA 2000 network was detected in 34 sites (Suppl. material 2). These included 11 sites located in South Aegean Islands, seven in Crete, five in Eastern Macedonia and Thrace, four in Central Macedonia and North Aegean Islands (respectively), two in Thessaly and one site in the Ionian Islands. No more than two species were identified from each site. *Lasius neglectus* and *T. immigrans* were each found in 10 NATURA 2000 sites. *Monomorium bicolor* and *P. indica* follow being present in six and four sites, respectively. *Nylanderia jaegerskioeldi* was found in only three sites situated in the South Aegean. *Cardiocondyla mauritanica* and *Hypoponera punctatissima* have been collected from two overlapping protected sites in Crete (GR4330003, GR4330007). Finally, *Tapinoma magnum* and *Tetramorium bicarinatum* have been collected from one protected site in South Aegean (Serifos Island) and Crete, respectively (Suppl. material 2).

Regarding the distribution of ants within different CLC types (Fig. 2), the majority of alien ants (48%) have been collected from artificial surfaces, including urban fabric (continuous and discontinuous) and artificial, non-agricultural vegetated areas such as green urban areas and sport and leisure facilities (Suppl. material 1). Furthermore, 28% of specimens have been collected from agricultural areas (mostly heterogeneous) including permanent crops and arable land. Around one fifth (21%) of records have penetrated forests and semi-natural areas with scrub and/or herbaceous vegetation associations being most common. Lastly, only two records of *T. immigrans* were found in wetlands, specifically within salt-marshes and three coastal records were classified by the analysis as within water bodies.

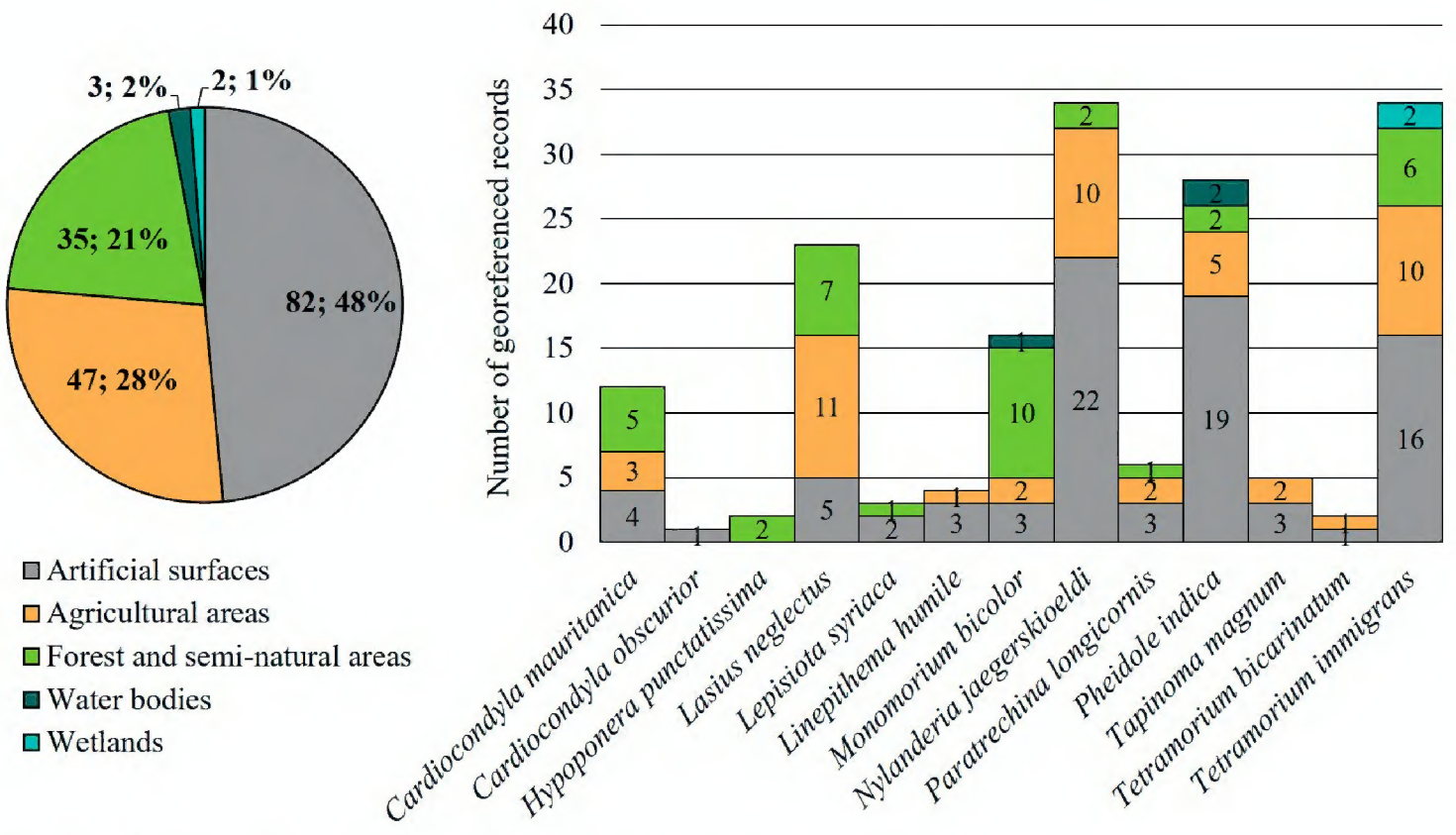

Figure 2. Corine Land Cover types occupied by alien ant species in Greece.

Discussion

Annotated checklist with comments on biology and distribution

Dolichoderinae

***Linepithema humile* (Mayr, 1868)**
Fig. 3

Literature records. Bernard (1967) (Greece); Radchenko (2007) (Crete); Salata et al. (2019) (Attica, Corfu, Crete, Peloponnese); Salata et al. (2020) (Crete); Borowiec and Salata (2013) (Peloponnese), (2021a) (Corfu).

Georeferenced records. Suppl. material 1.

Invaded administrative divisions. Attica, Crete, Ionian Islands, Peloponnese (4).

Notes. An alien species classified as one of the world's 100 worst invasive alien species (GISD 2022), with severe ecological impacts on native biodiversity recorded around the world (Wetterer et al. 2009). In Europe, *L. humile* has been reported to harm native vertebrate and invertebrate species (Cammell et al. 1996; Carpintero 2003; Carpintero et al. 2005; Wetterer et al. 2006; Alvarez-Blanco et al. 2017; Centorame et al. 2017; Zina et al. 2020) as well as reported as a household pest, infesting disturbed agricultural, urban areas and some natural habitats (Espadaler and Gómez 2003; Carpintero et al. 2004; Wetterer et al. 2009; López-Collar and Cabrero-Sañudo 2021). Such environments may act as "reservoirs" enhancing the survival and further spread of the species to natural habitats, protected areas and climatically non-optimal regions in higher latitudes (Carpintero et al. 2004; Roura-Pascual et al. 2004; López-Collar and Cabrero-Sañudo 2021), as already predicted for other alien Hymenoptera such as *Sceliphron curvatum* (F. Smith, 1870) in Europe (Polidori et al. 2021). In Greece, it has been collected from only a handful of urban and agricultural localities (Salata et al. 2019; present study). Nevertheless, given its invasion potential and recorded impact on native biodiversity further monitoring and studies on impacts are necessary.

***Tapinoma magnum* Mayr, 1861**
Fig. 4

Literature records. Borowiec et al. (2022) (Thasos).

Georeferenced records. Suppl. material 1.

Invaded administrative divisions. Central Macedonia, Eastern Macedonia and Thrace, South Aegean (3).

Notes. A recently discovered alien ant, native to the Western Mediterranean, that has managed to invade urban disturbed areas in Belgium, France, Germany, the Netherlands, Slovenia and Switzerland through human activities (i.e. through ports and plant nurseries) (Seifert et al. 2017b; Seifert 2018; Bračko 2019). In Greece, it has been detected from the Cyclades, Central Macedonia and Thassos Island in Eastern Macedonia and Thrace (Borowiec et al. 2022). So far, its presence has had no impact on the

Figure 3. Habitus of *Linepithema humile* (Mayr, 1868) in lateral view above and its known distribution in Greece below.

native fauna of occupied Greek sites. According to Seifert et al. (2017b), *T. magnum* in the Mediterranean can be mostly found in "open unstable or degraded areas with significant to very strong anthropogenic influence and a weakly developed tree layer". In Greece, despite the small number of collection sites, the species was collected from artificial surfaces such as parks and one agricultural area (path in meadow with walnut and fruit trees in Thassos) (Suppl. material 1) (Borowiec et al. 2022).

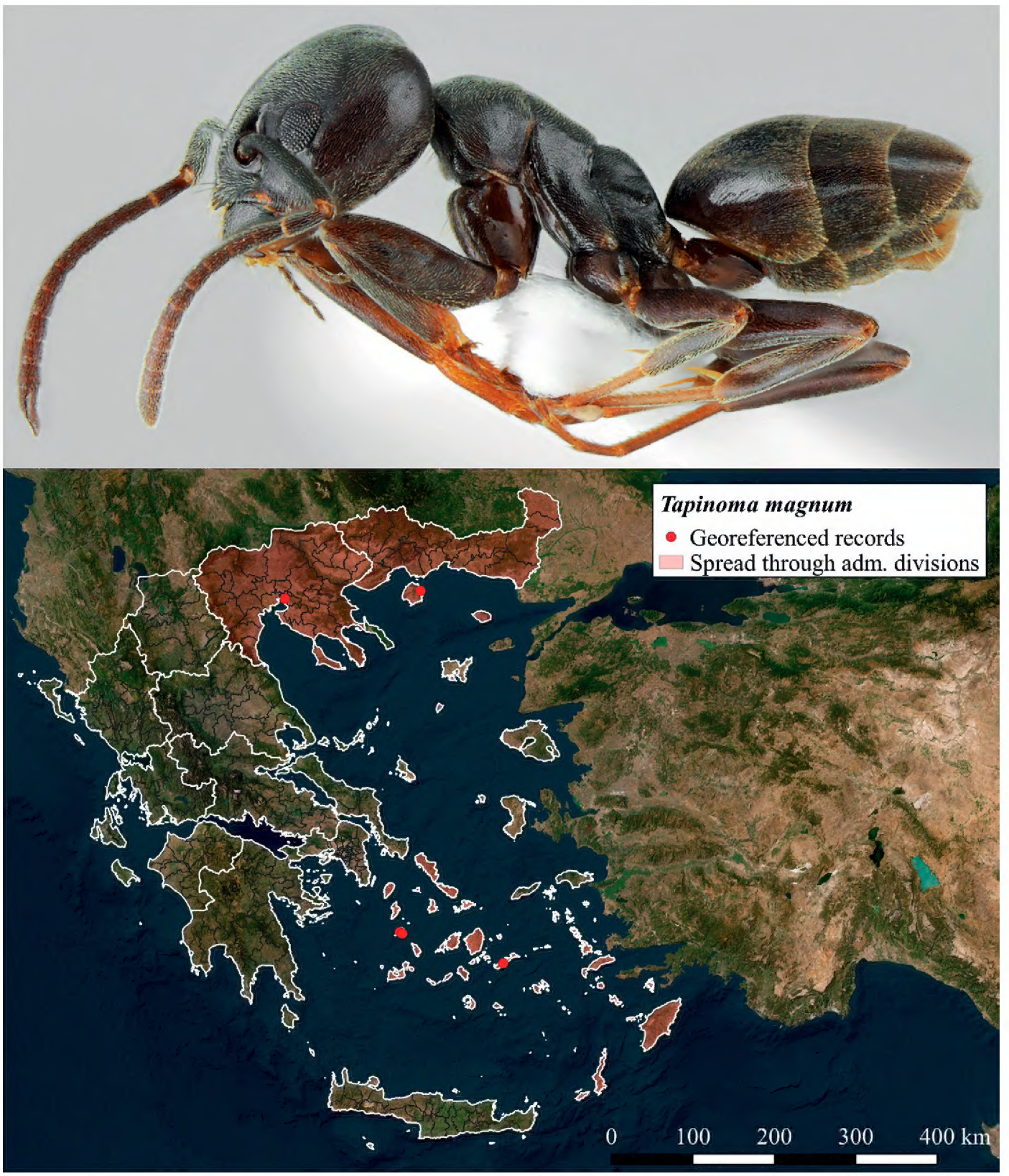

Figure 4. Habitus of *Tapinoma magnum* Mayr, 1861 in lateral view above and its known distribution in Greece below.

Formicinae

Lasius neglectus Van Loon, Boomsma & Andrasfalvy, 1990

Fig. 5

Literature records. Bračko et al. (2016) (Thrace), Borowiec and Salata (2017) (Peloponnese) [as *Lasius neglectus/turcicus* complex]; Seifert (2020) (Rhodes).

Georeferenced records. Suppl. material 1.

Invaded administrative divisions. Eastern Macedonia and Thrace, North Aegean, Peloponnese, South Aegean (4).

Figure 5. Habitus of *Lasius neglectus* Van Loon, Boomsma & Andrasfalvy, 1990 in lateral view above and its known distribution in Greece below.

Notes. The radiation centre of *L. neglectus* is probably situated in Asia Minor (Seifert 2015, 2020) or Central Asia (Turkmenistan and Uzbekistan) (Stukalyuk et al. 2020; AntWiki 2022). Records from Greece have been re-evaluated upon previously reported indistinct records of the *Lasius neglectus*/*turcicus* complex. Sporadic records have been obtained from the Aegean Islands, and the Peloponnese, and noticeably more populations in Eastern Macedonia and Thrace region. *Lasius neglectus* appears

in both urban and agricultural areas (Fig. 2), although according to our analysis it has managed to spread to forest and semi-natural areas including mixed, broad-leaved forests and natural grasslands of Eastern Macedonia and Thrace and the Aegean Archipelago (Suppl. material 1). Nevertheless, human-induced habitat modifications have been observed in all localities from which the species has been collected, in contrast to localities of native *Lasius turcicus* Santschi, 1921.

Paratrechina longicornis (Latreille, 1802)

Fig. 6

Literature records. Kugler (1988) (Greece); Tseng et al. (2019) (Rhodes); Borowiec et al. (2021) (Rhodes, Kalymnos).

Georeferenced records. Suppl. material 1.

Invaded administrative divisions. South Aegean (1).

Notes. A synanthropic species, collected from only two South Aegean Islands (Kalymnos and Rhodes) within the Dodecanese Archipelago. Despite its expected presence in urban and agricultural sites, a population was collected by Tseng et al. (2019) from a site classified as a natural grassland during the CLC analysis. This site corresponds to an archaeological site in Lindos (Rhodes), which shows that despite reaching more natural habitats the species still exhibits synanthropic behaviour and has not managed to spread to purely undisturbed habitats.

Nylanderia jaegerskioeldi (Mayr, 1904)

Fig. 7

Literature records. Menozzi (1932) (Rhodes); Collingwood (1993) (Karpathos); Borowiec and Salata (2012) (Peloponnese), (2014) (Kefalonia), (2018b) (Euboea), (2018d) (Zakynthos); Salata et al. (2019) (Attica, Crete, Karpathos, Kos, Rhodes); Salata et al. (2020) (Crete).

Georeferenced records. Suppl. material 1.

Invaded administrative divisions. Attica, Central Greece, Crete, Ionian Islands, North Aegean, Peloponnese, South Aegean (7).

Notes. One of the most widespread alien ants in Greece (Table 2; Fig. 7). Its range currently encompasses the Aegean Islands, Southern Greece and the Ionian Archipelago. Most collection sites correspond to urban and agricultural areas (Fig. 2). Nevertheless, two semi-natural areas have been invaded, including a natural grassland in Kefalonia Island (Ionian Archipelago) and sclerophyllous vegetation in Karpathos Island (Aegean Archipelago) (Suppl. material 1). Given its invasion potential further monitoring and studies on impacts are necessary.

Lepisiota syriaca (André, 1881)

Fig. 8

Literature records. Stitz (1928) (Crete); Salata et al. (2019) (Attica, Leros, Telendos).

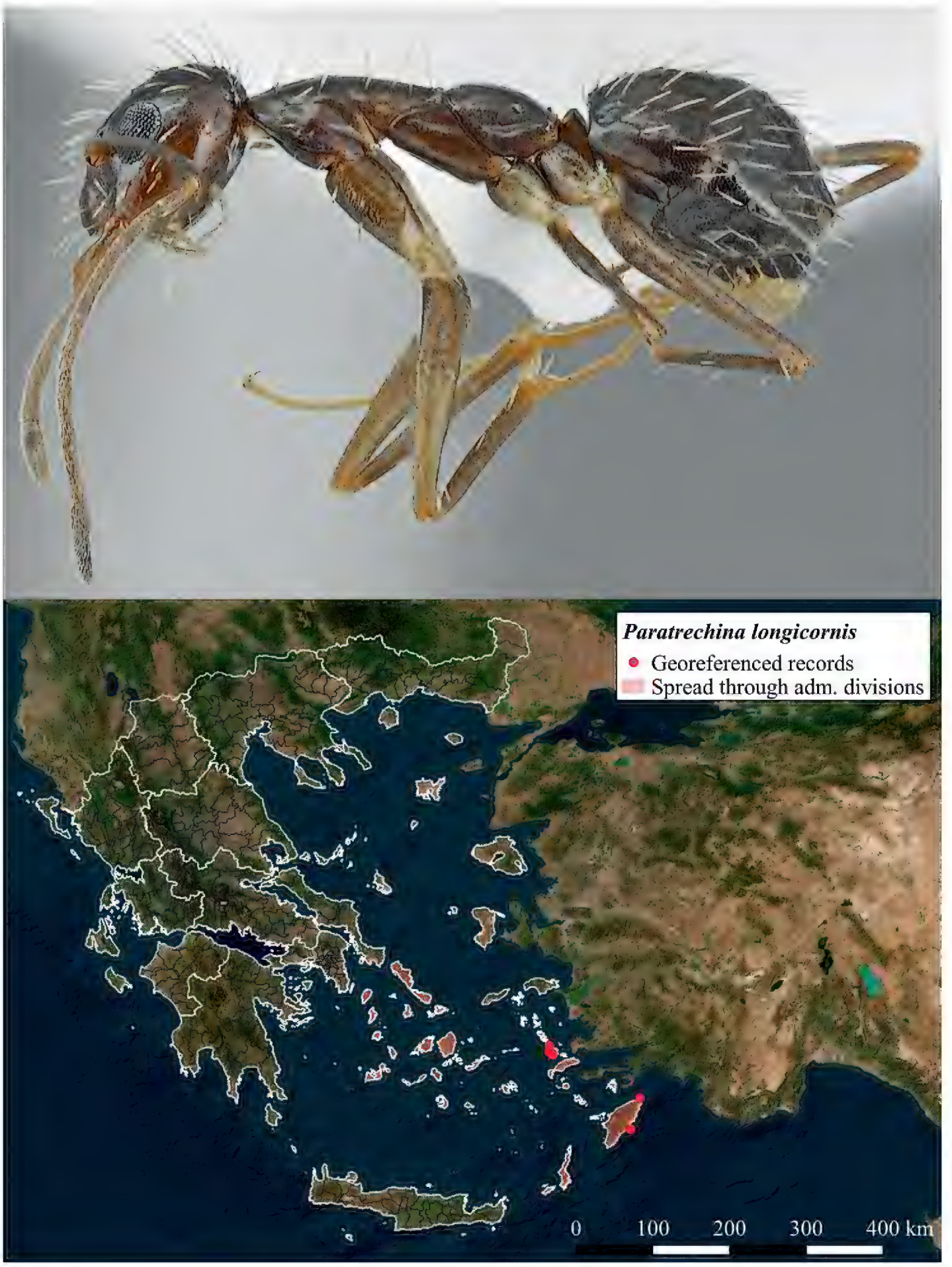

Figure 6. Habitus of *Paratrechina longicornis* (Latreille, 1802) in lateral view above and its known distribution in Greece below.

Georeferenced records. Suppl. material 1.

Invaded administrative divisions. Attica, Crete, South Aegean (3).

Notes. The alien status of the species in Greece is problematic, while the taxonomic identity of the whole *Lepisiota fraudenfeldi* group is also unclear. Thus, specimens

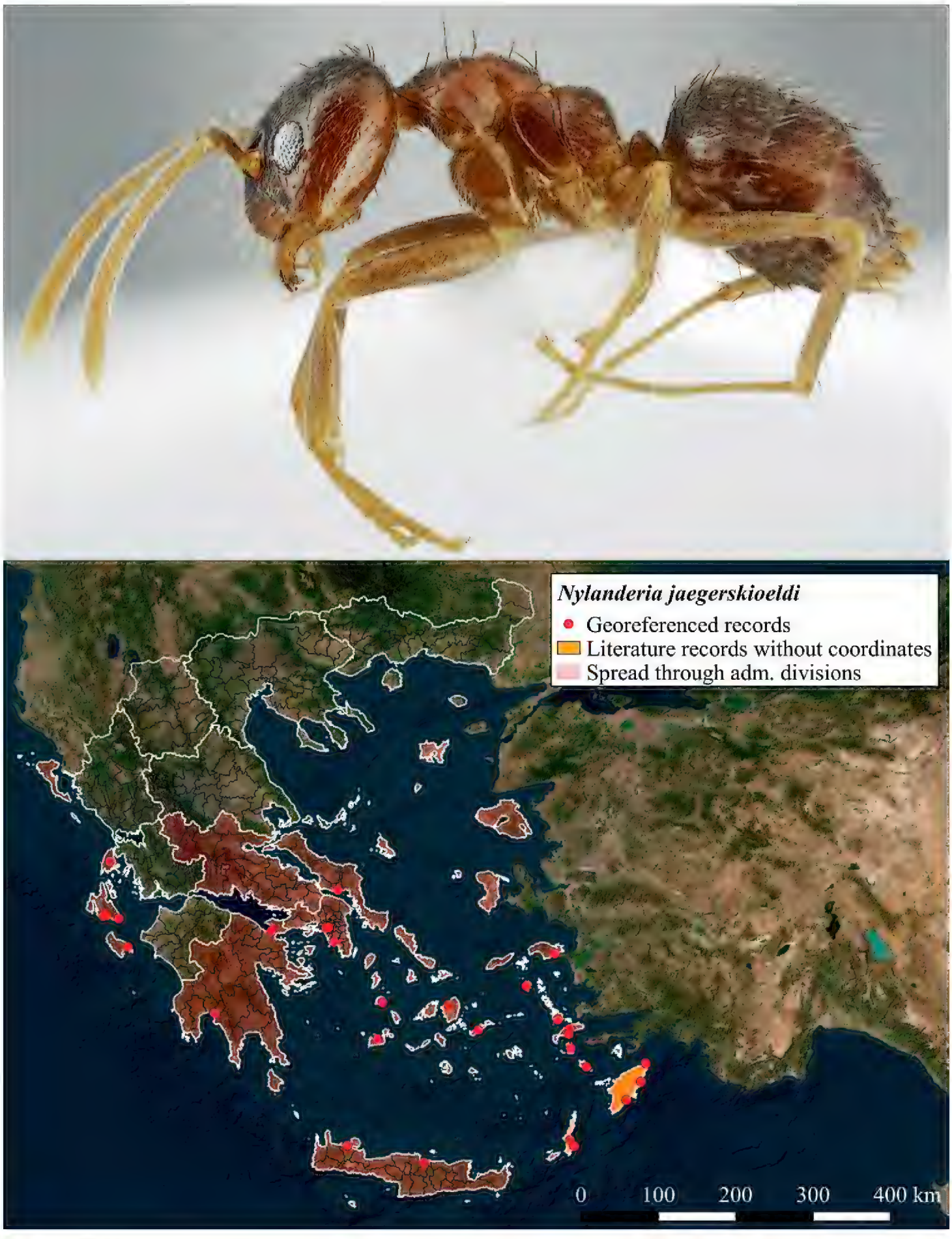

Figure 7. Habitus of *Nylanderia jaegerskioeldi* (Mayr, 1904) in lateral view above and its known distribution in Greece below.

identified as *Lepisiota* cf. *syriaca* sp. 1 (Borowiec and Salata 2012), were excluded. *Lepisiota syriaca* is regarded as native to the Near East and it is known only from Anatolia in neighbouring Turkey (Kiran and Karaman 2020). Its absence from Aegean Turkey,

Figure 8. Habitus of *Lepisiota syriaca* (André, 1881) in lateral view above and its known distribution in Greece below.

combined with its peridomestic lifestyle in Greece, may suggest its man-mediated introduction to the country. Thus, the species is maintained in the checklist of alien ants of Greece awaiting further investigations.

Myrmicinae

***Pheidole indica* Mayr, 1879**
Fig. 9

Literature records. Forel (1910) (Sporades); Finzi (1939) (Milos); Collingwood (1993) (Chios, Karpathos, Santorini, Zakynthos); Legakis (2011) (Crete, Cyclades, Dodecanese, Eastern Aegean, Ionian Islands); Borowiec and Salata (2012) (Crete, Rhodes), (2013, 2017) (Peloponnese); Salata et al. (2019) (Crete, Naxos, Karpathos, Kos, Rhodes), (2020) (Crete); Borowiec et al. (2021) (Kalymnos, Karpathos, Kos, Patmos, Rhodes, Tilos); Scupola (2021) (Peloponnese).

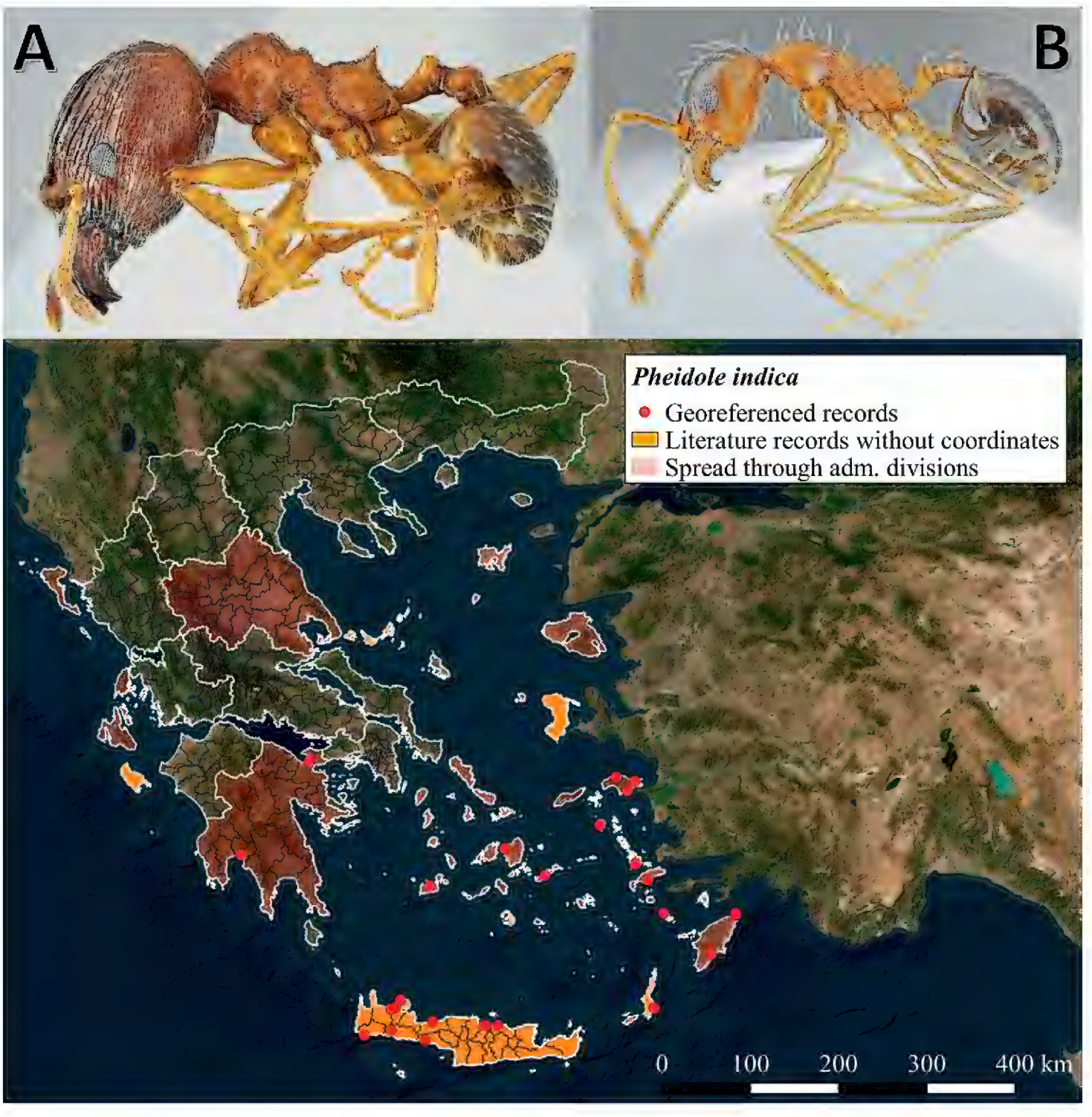

Figure 9. A Habitus of *Pheidole indica* Mayr, 1879 major and **B** minor worker in lateral view **C** known distribution in Greece.

Georeferenced records. Suppl. material 1.

Invaded administrative divisions. Crete, Ionian Islands, North Aegean, Peloponnese, South Aegean, Thessaly (6).

Notes. A widespread alien ant species collected from Greek islands and coastal areas of the Peloponnese (Fig. 9). It is predicted to occupy most of Southern Greece including Attica and Euboea Island in Central Greece. According to Sarnat et al. (2015), it is not considered to negatively affect native biodiversity or agriculture although its extensive spread and presence in a variety of habitats (Fig. 2; Suppl. material 1) dictates the necessity for further studies to assess its possible adverse impacts.

Strumigenys membranifera (Emery, 1869)

Fig. 10

Literature records. Agosti and Collingwood (1987) (Greece); Salata and Borowiec (2018) (Epirus).

Georeferenced records. None.

Invaded administrative divisions. Epirus (1).

Notes. Only one record from Greece (Arta-Metsovo) confirms the previous literature record of Agosti and Collingwood (1987) (Fig. 10). Further studies regarding its spread and impacts are necessary.

Cardiocondyla mauritanica Forel, 1890

Fig. 11

Literature records. Seifert (2003) (Crete, Paros); Borowiec and Salata (2012) (Crete, Rhodes); Salata et al. (2019) (Crete, Kos), (2020) (Crete); Borowiec et al. (2021) (Kalymnos, Kos, Rhodes).

Georeferenced records. Suppl. material 1.

Invaded administrative divisions. Attica, Crete, Ionian Islands, North Aegean, South Aegean (5).

Notes. Presumably native to Northern Africa, *C. mauritanica* is a xerothermophilous species found both in natural and man-made habitats (Seifert 2003; Wetterer 2014; Carpintero and Reyes-López 2014; Schifani and Alicata 2018; present study). In Greece, it has been collected from artificial, agricultural, semi- and natural habitats including protected areas (Suppl. materials 1, 2), although no negative impacts on native ants have been observed as in Spain, where it is not considered invasive (Carpintero and Reyes-López 2014). Its habitat preferences seem to overlap those of alien invasive *L. humile*, with which it has been found to co-exist (Ward 2005; Gulmahamad 1997; Gómez and Espadaler 2006; Heinze et al. 2006; Wetterer 2014). Wetterer (2012), mentioned that dominant invasive ant species such as *P. megacephala* and *L. humile* may benefit alien *Cardiocondyla* spp. through the exclusion of competing species.

Figure 10. Habitus of *Strumigenys membranifera* (Emery, 1869) in lateral view above [photographed by April Nobile, from www.antweb.org (AntWeb CASENT0173252)] and its known distribution in Greece below.

Cardiocondyla obscurior Wheeler, 1929

Fig. 12

Georeferenced records. Suppl. material 1.

Invaded administrative divisions. South Aegean (1).

Figure 11. Habitus of *Cardiocondyla mauritanica* Forel, 1890 in lateral view above and its known distribution in Greece below.

Notes. A cosmopolitan tramp species presumed native to Indomalaya (Wetterer 2015), being known from Egypt and countries of the Levantine coast in the Eastern Mediterranean (Donisthorpe 1930; Mohamed et al. 2001; Seifert 2003; Janicki et al. 2016). A single specimen of this species was collected from a table at a restaurant in the Old Town of Rhodes city (Fig. 12). In Europe, its outdoor locations are strictly restricted to urban sites (Espadaler and Ortiz de Zugasti 2019). *Cardiocondyla obscurior*

Figure 12. Habitus of *Cardiocondyla obscurior* Wheeler, 1929 in lateral view above and its known distribution in Greece below.

is considered an arboreal species nesting in tree cavities and plant structures above ground (Espadaler and Ortiz de Zugasti 2019).

***Tetramorium bicarinatum* (Nylander, 1846)**
Fig. 13

Literature records. Salata et al. (2019, 2020) (Crete).

Georeferenced records. Suppl. material 1.

Figure 13. Habitus of *Tetramorium bicarinatum* (Nylander, 1846) in lateral view above and its known distribution in Greece below.

Invaded administrative divisions. Crete (1).

Notes. The species has been collected only once from an urban site on Crete island (Heraklion). A recent citizen-science record from an agricultural area of Chania (Crete),

spotted on iNaturalist (2022) (https://www.inaturalist.org/observations/126973273) reinforces a hypothesis of widespread, established populations on the island in anthropogenic habitats.

Tetramorium immigrans Santschi, 1927

Fig. 14

Literature records. Wagner et al. (2017) (Central Macedonia, Crete, Peloponnese, Samos, Thasos); Borowiec and Salata (2018d) (Zakynthos), (2021a) (Corfu); Salata and Borowiec (2019a) (Corfu, Crete, Central Macedonia, Eastern Macedonia and Thrace, Peloponnese, Rhodes, Thessaly), (2019b) (Zakynthos); Salata et al. (2020) (Crete); Borowiec et al. (2021) (Patmos, Rhodes).

Georeferenced records. Suppl. material 1.

Invaded administrative divisions. Central Greece, Central Macedonia, Crete, Eastern Macedonia and Thrace, Ionian Islands, North Aegean, Peloponnese, South Aegean, Thessaly, Western Greece (10).

Notes. The most widespread alien ant in Greece extending its occurrence in 10 out of 14 Greek administrative divisions (Table 2; Fig. 14) (although its presence throughout the country should be expected). Until recently the taxonomic status of cryptic species within the *Tetramorium caespitum* complex was problematic. Wagner et al. (2017) unveiled the extended spread of this alien species, probably native to Anatolia and Caucasus region, in most of Europe invading not only anthropogenic but also natural habitats. Among its adverse ecological impacts, it can hybridise with the native to Greece *Tetramorium caespitum* (Linnaeus, 1758) (Wagner et al. 2017) and has been recently observed employing soil dropping to compete against native ants in Sicily (Schifani et al. 2022). Nevertheless, its impacts on native biodiversity and human activities have been characterised as mild and its potential "ability to displace native ant species is understudied but questionable" (Moss et al. 2022). Further studies are needed to assess the environmental impacts of this alien ant on native biodiversity given its collection from both man-made and natural habitats (Fig. 2).

Monomorium bicolor Emery, 1887

Fig. 15

Literature records. Menozzi (1928) (Karpathos), (1936) (Alimia, Kalymnos, Karpathos, Kasos, Kos, Rhodes, Telendos); Agosti and Collingwood (1987) (Greece); Collingwood (1993) (Karpathos); Salata et al. (2019) (Crete, Karpathos), (2020) (Crete); Borowiec et al. (2021) (Astypalaia, Karpathos, Ofidousa, Thira).

Georeferenced records. Suppl. material 1.

Invaded administrative divisions. Crete, South Aegean (2).

Notes. Records of Legakis (2011) were excluded upon examination of material and its identification as *M. subopacum* (Salata et al. 2019). The current known distribution of *M. bicolor* includes Crete and South Aegean Islands (Fig. 15). It is a thermophilous, synanthropic species inhabiting arid regions and disturbed habitats, although

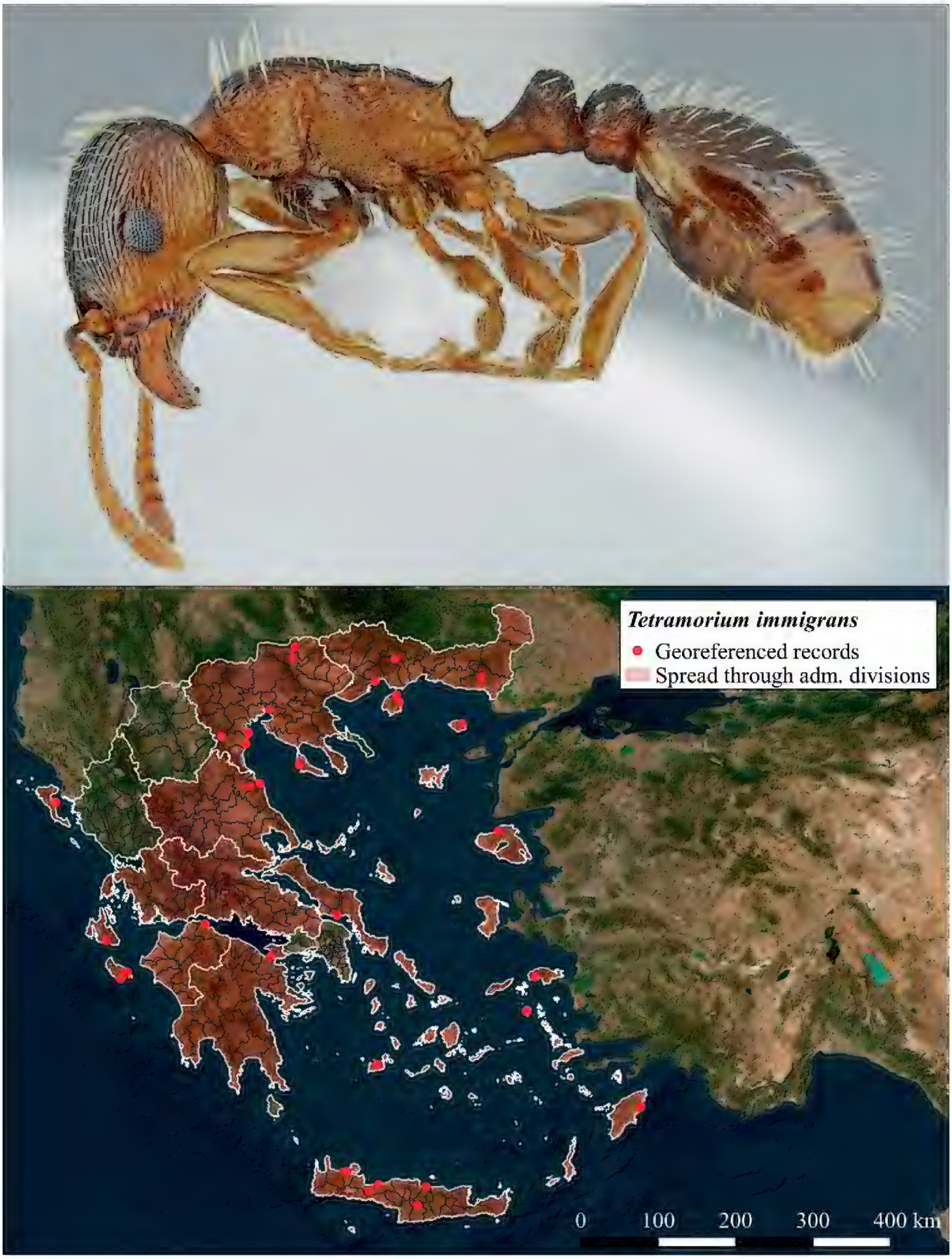

Figure 14. Habitus of *Tetramorium immigrans* Santschi, 1927 in lateral view above and its known distribution in Greece below.

many populations have been collected from forest and semi-natural areas particularly scrub and/or herbaceous vegetation associations such as natural grasslands and sclerophyllous vegetation (Fig. 2).

Figure 15. Habitus of *Monomorium bicolor* Emery, 1887 in lateral view above and its known distribution in Greece below.

Monomorium pharaonis (Linnaeus, 1758)

Fig. 16

Literature records. Menozzi (1928) (Rhodes); Bolton (1987) (Central Macedonia, Crete).

Georeferenced records. None.

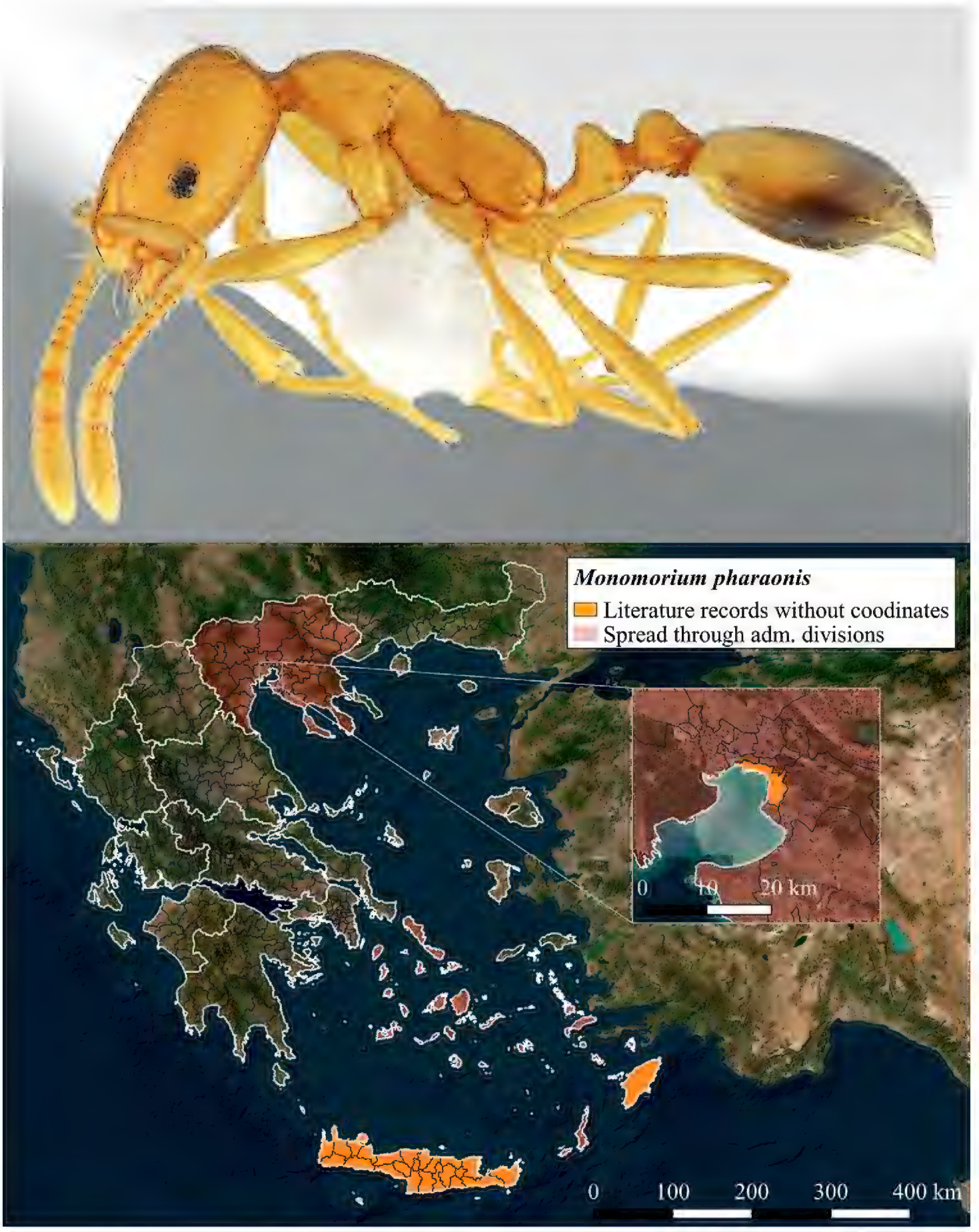

Figure 16. Habitus of *Monomorium pharaonis* (Linnaeus, 1758) in lateral view above and its known distribution in Greece below.

Invaded administrative divisions. Central Macedonia, Crete, South Aegean (3).

Notes. A synanthropic indoors introduced species. Since Bolton (1987), there is no recent available data on the species distribution in Greece. Further research on its presence, distribution and household impacts is necessary. Citizen-science initiatives

looking into ants in buildings and households could potentially help detection and management efforts. Further studies could also investigate the potential occurrence of the cryptic *Monomorium sahlbergi* Emery, 1898 (Boer et al. 2020).

Ponerinae

Hypoponera punctatissima (Roger, 1859)

Fig. 17

Literature records. Agosti and Collingwood (1987) (Greece); Legakis (2011) (Eastern Aegean).

Georeferenced records. Suppl. material 1.

Invaded administrative divisions. Crete, North Aegean (2).

Notes. Native to the Afrotropics, *H. punctatissima* has been deemed as the most accomplished alien ant species due to its worldwide spread (Bolton and Fischer 2011). The species inhabits both urban (gardens, crop fields) and natural habitats such as forests, where it has been collected from rotten wood and topsoil (Bolton and Fischer 2011). In Greece two specimens have been collected from a sandy beach area in Herakleion (Crete) and a deciduous forest in Rethymnon (Crete) (classified as natural grasslands by the CLC analysis in Fig. 2 and Suppl. material 1) (Fig. 17), although further research is needed to assess its distribution and impacts. Further studies could also investigate the potential occurrence of the cryptic *Hypoponera ergatandria* (Forel, 1893) (Seifert 2013).

Species excluded, previously reported as alien to Greece or records designated as dubious

Formicinae

Anoplolepis gracilipes (Smith F., 1857)

Notes. The species has been reported as present in Greece only by Radchenko (2007) in the Fauna Europaea (FE) website. Nevertheless, due to the absence of available material and bibliographic sources the species is not regarded as present in Greece (Salata et al. 2019). Its mention in FE is most probably erroneous as indicated in the case of other ant species in the database such as those indicated by Schifani and Alicata (2018) regarding Sicily.

Nylanderia vividula (Nylander, 1846)

Notes. The species has been reported only once from Rhodes Island (Dodecanese) (Forel 1888), while all European records have been reported from indoor localities (Trager 1984). Additionally, it was reported from Greece before the description of *N. jaegerskioeldi*, a

Figure 17. Habitus of *Hypoponera punctatissima* (Roger, 1859) in lateral view above and its known distribution in Greece below.

tramp species common in outdoors anthropogenic sites in this country. Given the absence of available material for examination we tentatively suggest that *N. vividula* is not present in Greece and Forel's record should be assigned to *N. jaegerskioeldi*.

Myrmicinae

***Aphaenogaster splendida* (Roger, 1859)**

Notes. A recently published review indicated that *Aphaenogaster splendida* is rare in Greece and its known distribution is limited to anthropogenic sites (Salata et al. 2021). Thus, it could also be an introduced species in this region. However, until this case is resolved based on molecular analyses we decided to treat it as native to Greece. According to Schifani (2019) "the definition of its native range remains unclear".

***Monomorium monomorium* Bolton, 1987**

Notes. A widespread species previously reported as alien to Greece (Salata and Borowiec 2018), which has been collected both from urban and natural habitats (Borowiec and Salata 2021b). Its extended distribution in Southern Europe, where the species is believed to be native, suggests that the species could be also native to Greece. Due to the perplexed taxonomy of the *M. monomorium* species group (Bolton 1987), further research is necessary to fully assess its native or alien status in the Mediterranean region.

***Monomorium subopacum* (Smith, 1858)**

Notes. Bolton (1987) assumed that it could be native to the Mediterranean where it is "very widely distributed but appears originally to have been a circum-Mediterranean species which has subsequently been spread by commercial activity". Upon reconsideration, the species should be regarded as native to Greece as considered to other Mediterranean countries (AntWiki 2022).

***Pheidole megacephala* (Fabricius, 1793)**

Notes. Specimens of *P. megacephala* collected from Greece have been deemed erroneous upon re-examination (Sarnat et al. 2015; Salata et al. 2019; Salata and Fisher 2022). A thorough investigation of numerous *Pheidole* specimens at the ZMUA collected from various points around Greece has provided no evidence of the presence of this species.

***Solenopsis geminata* (Fabricius, 1804)**

Notes. The sole record of the species in Greece dates back to 1993 when it was collected from Zakynthos Island in the Ionian Archipelago (Collingwood 1993). Since then, no specimens of this invasive alien species have been collected from the island, despite of additional sampling (Borowiec and Salata 2018d), nor from Greece in general. Due to the high polymorphism evidenced in the worker caste (Wetterer 2011) we hypothesize that records of *S. geminata* are dubious i.e. misidentifications of na-

tive species. Although the severe adverse environmental (competition and elimination of native ant communities from invaded habitats), economic (agricultural pest) and human-health impacts (stinging) associated with the species (Wetterer 2011) necessitate further research into its presence in Greece, we assume that almost thirty years after its initial detection, *S. geminata* should have further spread and its impacts would not go unnoticed. Alternatively, the species may have indeed reached the island of Zakynthos but did not manage to establish. In the absence of examined material from Collingwood's collection and its absence from Zakynthos during more recent collecting events (Borowiec and Salata 2018d), the species is removed from the checklist of alien ants of Greece.

Ponerinae

***Hypoponera eduardi* (Forel, 1894)**

Notes. Although reported as alien to Greece (Salata et al. 2019), *H. eduardi* may indeed be native to the country, as indicated by Bolton and Fischer (2011) by its continuous distribution in the Palaearctic across the Mediterranean. In addition, the species seems to occupy both urban and natural habitats. In the latter, it has been commonly found in well-irrigated and shaded areas, rich in organic matter e.g. deciduous forests and streams (Borowiec and Salata 2017, 2018c, 2021a, 2022; Salata et al. 2019). Thus, we tentatively suggest its removal from the checklist of alien ants inhabiting Greece.

Spread throughout Greek administrative divisions

The number of alien ant species seems to increase from North to South (Fig. 1). Two hypotheses, not mutually exclusive, are suggested. On the one hand, the tropical and subtropical origin of the majority of alien ants (Table 1), may render climatic conditions more optimal in the Southern regions rather than the Northern administrative divisions, with the majority of alien ant species being collected from Southern Greece, especially from the Aegean Archipelago (Fig. 1). Indeed, as evidence shows, the island locations, as well as areas around the Peloponnese, are scoring higher on TDI (Thom's discomfort index), which in essence represents a higher air temperature and higher humidity level envelope (Kambezidis et al. 2021). This seems to be even the trend for the near future based on climate change scenaria assessments (Tzanis et al. 2019). According to our second hypothesis, this can be partly attributed to sampling biases with more myrmecological studies carried out on Greek Islands compared to the mainland. Nevertheless, these observations are in accordance with biogeographic analyses showing that islands are generally more species rich in alien species than the mainland, and that outside tropical regions the number of alien species decreases with latitude (Sax 2001; Pyšek and Richardson 2006). With islands being hotspots of established alien species (Dawson et al. 2017) and given the adverse impacts of biological invasions to island communities (Cole et al. 1992; O'Dowd et al. 2003; Wetterer and Porter 2003;

Abbott 2005; Wetterer et al. 2006; Reaser et al. 2007; Plentovich et al. 2009; Russell et al. 2017; Castro-Cobo et al. 2021) it is important to monitor spatiotemporal patterns of alien species and investigate their possible impacts on endemic island species. Additionally, the alien species richness of administrative divisions such as Attica and Central Macedonia may be significantly underestimated due to reduced collecting effort. After all, the number of established alien species has been shown to increase with GDP per capita, human population density and area (Dawson et al. 2017), with the two administrative divisions accounting for the highest numbers of inhabitants (five and one million, respectively) and GDP per capita. As such, the number of alien ant species in the aforementioned administrative divisions could be higher. However, it is important to add that these parameters cause a steeper rate of increase for alien species richness in the case of islands rather than mainland regions (Dawson et al. 2017).

Alien ants and land-use in Greece

Three quarters of the presented georeferenced records (76%) fall within urban and agricultural sites (Fig. 2). This indicates that alien ants in Greece can be mostly found in degraded, urbanised sites with intense human activity. This does not come as a surprise since the majority of alien terrestrial invertebrates have been found to inhabit human-made habitats, specifically parks and gardens, buildings and houses as well as agricultural and horticultural lands (Lopez-Vaamonde et al. 2010; Pyšek et al. 2010). Similarly, in the case of ants, the majority of recorded alien species has been found to inhabit urban sites (Espadaler and Bernal 2003; Schifani 2019; López-Collar and Cabrero-Sañudo 2021; Rosas-Mejía et al. 2021; present study), with large numbers of alien species collected from points of entry such as airports and ports, agricultural premises (e.g. greenhouses) as well as tourist facilities including botanical gardens and zoos (Boer and Vierbergen 2008; Jucker et al. 2009; Harada et al. 2014, 2016; Gochnour et al. 2019). Such anthropogenic habitats should be intensively surveyed throughout Greece in hopes of detecting novel alien ant species, deciphering their introduction pathways and further supplementing their known distribution. The lack of studies addressing both the socio-economic impacts of alien ants in man-made habitats and their ecological impacts in natural habitats and protected areas, constitute an impediment towards designing management strategies, effectively minimising their spread and mitigating their impacts.

Invasiveness, conservation and future research

Regarding the distribution of individual species (Table 2), the spread of *T. immigrans* and *N. jaegerskioeldi* to most of Greece is worrying given both their observed adverse impacts on native ant biodiversity (Wagner et al. 2017; Salata et al. 2019; Schifani et al. 2022) and occurrence within the NATURA 2000 network (Suppl. material 2). The resilience of protected areas against biological invasions has been recently assessed by Gallardo et al. (2017) and Liu et al. (2020), showing fewer established alien species in protected areas despite their habitat suitability, while generally established populations

of alien species can be found 10–100 km from their boundaries. Overall, nine alien ant species have managed to penetrate 34 NATURA 2000 sites in Greece (Suppl. material 2). Around one third of these sites are situated in Northern Greece (Thessaly, Central Macedonia, and Eastern Macedonia and Thrace = 11 sites), being invaded by *L. neglectus* and *T. immigrans*. The remaining species and further records of *L. neglectus* were collected from protected areas in Southern Greece (Aegean region), where the majority of alien ant species are distributed (Table 1). Although restricted to a few urban areas, *L. humile* also represents a worrying case for the myrmecofauna of Greece and requires further monitoring. A quantitative assessment, including the use of bait traps and structured pitfall sampling, could potentially shed light on their impacts on native ant community assemblages. Such studies could be extended to assess all alien ant species of Greece in both urban and natural sites, including protected areas and their environs.

In addition, citizen-science initiatives could be integrated into the study of alien ants. Despite their small body size and need of expert knowledge for their robust identification, which both constitute impediments to the application of citizen-science approaches (Caley et al. 2020), high-quality photographic material of alien ants such as the presented record of *T. bicarinatum* from Crete or citizen-science records of morphologically discrete species (e.g. *A. gracilipes* and *L. humile*) can supplement the distribution of invasive ant species, especially within urban habitats (Ward 2014; López-Collar and Cabrero-Sañudo 2021; Vásquez-Bolaños and Wetterer 2021). Furthermore, the collection of ant specimens by the public, in the context of organised BioBlitz events or structured citizen-science projects, could further enhance detection efforts, raise public awareness on biological invasions of ants and minimise taxonomic biases (Castracani et al. 2020; Silva-Rocha et al. 2020; Meeus et al. 2021).

Conclusions

In total, 15 alien ant species are currently distributed in Greece (Table 1). Based on historical records, eight additional species have been reported, although their records are deemed dubious or these species have been proved to be native. *Cardiocondyla obscurior* is presented for the first time for Greece. Nevertheless, the presence of widely distributed alien species such as *Trichomyrmex destructor* (Jerdon, 1851) (Wetterer 2009a), *Tapinoma melanocephalum* (Fabricius, 1793) (Wetterer 2009b), as well as the invasive *Brachyponera chinensis* (Emery, 1895) (Menchetti et al. 2022), and *W. auropunctata* gradually spreading throughout the Mediterranean (Vonshak and Ionescu-Hirsch 2009; Vonshak et al. 2009, 2010; Espadaler et al. 2018, 2020; Demetriou et al. 2022), should be further investigated. This updated, commented checklist and analyses aim to provide an overview of the alien ants of Greece in order to enhance any necessary monitoring and strategic planning against invasive alien species, while simultaneously indicating future research needs.

The species richness of alien ants seems to be higher as we move from North to South; alien ants also seem to prefer anthropogenic habitats although some species have managed to penetrate natural and protected areas. Further research is needed to

address the adverse environmental and socioeconomic impacts of alien ants in Greece, especially in sensitive island habitats and protected areas.

Dichotomous, online identification tools and educational material for protected areas' officials as well as customs control officers could potentially enhance rapid response and early warning systems, thus preventing new arrivals and further spread of alien ants. Such tools would be particularly important for invasive alien species with the potential to harm native biodiversity, socioeconomic parameters and human-health, yet to be found from Greece. For example, *S. geminata*, *S. invicta* Buren, 1972, *S. richteri* Forel, 1909 and *W. auropunctata*, which have been recently added to the list of invasive alien species of EU concern (EU2022/1203) (Rabitsch 2022a, b). Molecular analyses assessing the genetic diversity of alien ants inhabiting Greece could shed light on their invasion history and introduction pathways.

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Supplementary material 1

Georeferenced records of alien ants in Greece

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Data type: occurences

Link: https://doi.org/10.3897/neobiota.86.98157.suppl1

Supplementary material 2

Distribution of alien ants in NATURA 2000 sites

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Data type: occurences

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